

A CONTRIBUTION TO THE DEVELOPMENT OF THE
COMMON PHALANGER.

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(Plates XXII.-XXV.)

It seems at first sight somewhat surprising that so little work has been done towards the developmental history of Marsupials, considering the important position occupied by this group, and the number of points on which light might be thrown on the structure and development of the higher mammals. But doubtless one of the chief reasons is that marsupials only breed once or at most, I believe, twice a year, and that the periods of gestation are so short that it is exceedingly difficult for even those on the spot to obtain a good collection of intra-uterine stages. As this difficulty will always exist and the chances are rather against any one collector obtaining a large series of intra-uterine stages of certain forms, it seems advisable that those who are in a position should fill up what gaps they can rather than wait till some one is able to give an exhaustive treatise.

The difficulties in the way of collecting a series of early stages are not so very great in the case of one or two of the larger forms, but in many others they are considerable, and this is the case with the common Phalanger; so that, though it is one of the commonest of marsupials, scarcely anything has been published on its development. Selenka* in 1891 gave an account of some early stages of the ovum, and in 1897 Beard† published an account of two of my embryos—one shortly before birth and the other just

* Selenka, E., Studien zur Entwickl. der Thiere, Hft. 5.

† Beard, J., "The Birth-period of *Trichosurus vulpecula*," Zool. Jahrb. 1897.

born; with the exception, however, of these two papers and of one or two dealing with some special point in the anatomy* I am not aware of anything else having been published on the development of this form. Nor indeed has there apparently been any account published of the development of the intra-uterine embryo in any diprotodont marsupial.

From the autumn, 1894, till May, 1896, I was engaged in the practice of my profession at Taralga, N.S.W., a little township situated on the Blue Mountains about 30 miles N.W. of Goulburn. Originally the whole country round had been covered by the monotonous gum-trees, and though much of the land has now been cleared much still remains in a virgin condition, and in many parts the trees have only been thinned. These woodlands afford shelter to a variety of marsupials, of which the common Phalanger, popularly called the "Possum" (*Trichosurus vulpecula*), is the most abundant, although some years ago the Native Bear (*Phascolarctus cinereus*) is said to have been more plentiful. Within the last two years, owing to the high price of skins, the phalangers have been shot in such numbers that I understand they have now become scarce.

The phalanger comes out of its retreat shortly after the sun is set, and may occasionally be seen running about before the daylight has quite died away; but as a rule it is only on moonlight nights that the animal is to be seen. The general opinion among those who shoot phalangers for their skins is that the animals usually spend the early part of the night on the ground, only running up the trees when disturbed, but that after midnight they for the most part remain among the branches. This is probably correct, and when hunting one or two dogs are usually taken to prowl about and chase the phalangers up the trees. When their barking announces a find the hunter hastens up, and on careful

* Broom, R., "Is there a critical period in Marsupial development?" Journ. Anat. and Phys. Vol. xxxii. 1898; "On the arterial arches and great veins in the fetal Marsupial," Journ. Anat. and Phys. Vol. xxxii. 1898; "On the existence of a sterno-coracoidal Articulation in a fetal Marsupial," Journ. Anat. and Phys. Vol. xxxi. 1897.

examination he probably sees the little animal sitting on one of the higher branches, from which, with a well-aimed shot, there is little difficulty usually in dislodging it. Should the animal be merely wounded, it is not improbable that it may hang suspended by its prehensile tail, and occasionally it may continue so to hang after it is quite dead, especially if it has managed to catch its tail round a small twig. Except during the pairing season the animals are usually seen singly. The ring-tailed phalangers (*Pseudochirus*) and the great flying phalangers (*Petauroides*) are, on the other hand, generally found in pairs.

About the month of March the phalanger begins to breed, though there is apparently some little difference in the exact breeding season in different years. Thus in 1896 the majority of the females had their young three or four weeks earlier than in 1895. Though there are two teats in the pouch there is almost never more than one young one at a time. My friend Mr. Walter Scott, of Golspie, who has rendered me most valuable assistance in the collection of specimens, and to whose kindness I owe most of my intra-uterine stages, though he has shot many thousands of phalangers, has only on one occasion come across a case of twins, which he kindly sent me with the pouch.

The exact period of gestation and the rate of growth of the fetus could only be found with certainty by breeding in captivity, but by taking into consideration the average degree of development at different dates the rate of growth can be approximated. For though there are individuals which have their young some weeks later and others earlier than the rest, the large majority agree very closely in their time of breeding. Thus on 11th May, 1895, out of 12 females shot 10 had mammary fetuses varying from 20 to 70 mm. in length, but averaging 40 mm., while two had ova in the uterus in early segmentation and primitive streak stages. By the following moon—for, of course, after a week's shooting by one moon nothing further can be done till nearly three weeks—most of the young averaged from 60-85 mm., while in the beginning of July the mammary fetuses averaged from 100-130 mm. By August the little one is well furred and able

to leave the pouch, though for probably another month at least the little one returns to the pouch for milk; and even after the young is too large for the pouch it keeps by its mother till nearly full grown. By the following March or April the previous year's young are full grown and ready to start families of their own.

In connection with the breeding habits Mr. Scott sends me the following very interesting note, which confirms my own opinion, and to some extent explains the difficulty in obtaining intra-uterine embryos:—"Just before giving birth to their young," he says, "the female opossums are not out very much. My reason for making this assertion is this—during the moon in the beginning of April [full moon was on 6th April] when most of the females were on the point of having their young, I found very few does—nearly $\frac{3}{4}$ of those got being bucks—whilst during the moon just past [full moon 6th May] most of those shot were does, but, unfortunately, they had, with very few exceptions, already their young ones in the pouch."

As I have only a very few very early stages, and as Selenka has already described very similar ova of the Rat-Kangaroo, I shall in the present communication confine myself to descriptions of the later intra-uterine embryos, with some notes on the mammary fetuses. As the membranes in most of the stages described have been torn and displaced, and are in only one case moderately intact, I shall not refer to these structures at present, beyond remarking that in the case referred to, that of embryo D, I can find no trace of a placenta, nor does the allantois appear to reach the uterine mucous membrane.

Description of Embryos.

EMBRYO A (8.5 mm.). Plate XXII., fig. 1.

I have thought this embryo worthy of description, notwithstanding the unfortunate circumstance that the front of the head is wanting, as on the whole the internal organs are very well preserved, and many of them are in a very interesting stage of development.

External anatomy.—As figured the fœtus measures 8·2 mm., so that allowing for a slight crushing of the back of the head, the uninjured fœtus probably measured 8·5 mm. The most striking characteristic of the external appearance is the great proportional development of the fore-quarters; while the hind limbs are little more than buds, without any indication of digits; the fore limbs are well developed, and have digits distinctly divided from each other, though not completely. Each digit is somewhat pointed, and on section there are found to be distinct indications of the developing claws. The anterior limbs are short and stout, and, as seen from the front, are pretty widely apart, which is owing to the skeletal elements of the two sides not having yet met in front of the heart. The tail is moderately stout, and towards the tip the spinal cord is distinctly seen through the thin epidermis.

Epidermis.—The epidermis, though thin, is not uniformly so. On the fore-limbs and back there is a very distinct epitrichial layer, but towards the lower part of the body and in front it is much less marked, and in some parts not very distinct. Claw rudiments are well marked at the tips of the anterior digits.

Skeleton.—The injured condition of the head makes it impossible to say much more than that the parachordal cartilages are well formed, and that there is as yet no chondrification of the auditory capsule. Sufficient of Meekel's cartilage is preserved to show that it is distinctly chondrified, although in the hyoid arch the process is just commencing. In the cervical region the vertebral centra and arches are already cartilaginous, and cartilage can be recognised in the vertebral centra down to the upper lumbar region. The upper ribs are fairly well chondrified, although no distinct sternum is as yet present. The scapula is well developed, as are also the elements of the fore limbs, but the coracoid is only distinctly formed at its outer part. In the clavicle ossification is just commencing. The skeletal elements of the pelvis and hind limbs are not yet distinctly differentiated.

Nervous system.—The central canal of the spinal cord is narrow in its anterior half, but its posterior half is on section oval or pear-shaped. The cellular elements are much more

numerous round the posterior half of the canal than in the anterior half. In the antero-lateral horn the group of neuroblasts from which the anterior roots are springing is comparatively small. Both anterior and posterior white columns are as yet small.

Heart and vessels.—The two auricles communicate freely in the upper part below the margin of the septum superius, but are divided below by the septum intermedium. The septum inferius does not reach the auriculo-ventricular ostium; the ventricles being thus in free inter-communication. The sinus venosus is comparatively small. The truncus arteriosus is undivided to the level of the upper third of the auricles. The condition of the main blood vessels I have recently elsewhere described.* It may here be briefly noted that the remains of the right aorta and of the right ductus arteriosus Botalli can still be traced, and that the right pulmonary artery comes off very distinctly from the right fifth (6th ?) arterial arch, the left pulmonary artery coming off as distinctly from the left arch. The condition of the umbilical veins is very interesting in that, though the embryo is in some respects more advanced than a six weeks' human embryo, there are still two umbilical veins present, the right being about as large as the left.

Lungs.—The degree of ramification of the bronchial tubes is about equal to that of a seven weeks' human fœtus, though the proportion of mesoblastic tissue into which the sprouting is taking place is considerably less.

Alimentary canal, &c.—The œsophagus is small and for a short distance in the neighbourhood of the aortic arch the lumen is lost. In the lower part the lumen is exceedingly small. The stomach and duodenum are well developed, but below the duodenum the lumen of the canal steadily diminishes, and for some distance in the neighbourhood of the vitelline duct, traces of which are still apparent, the lumen is absent. The canal continues very small

* R. Broom. "On the arterial arches and great veins in the foetal Marsupial." *Journ. Anat. and Phys.* Vol. xxxii. p. 477, April, 1898.

till it opens into the large intestine. There is a distinct and fairly large thimble-shaped caecum which is continuous with a moderately wide dilatation of the large intestine about three times as long as the caecum. From the upper end of this dilatation, however, the canal again narrows, and continues as a narrow tube to the cloaca. The liver is well developed, and already there is a distinct and well-formed gall bladder. The pancreas is fairly well developed.

Urinogenital system.—The mesonephros is of fairly large size, but the tubules and glomeruli are considerably smaller than in the Wolffian body of an embryo sheep in a somewhat similar stage of development. The peritoneal funnels of the Muellerian ducts are developed, but the ducts themselves have scarcely commenced. The germinal epithelium forms a comparatively narrow layer. The kidney and ureter are already indicated and differentiated from each other, the kidney being present as a somewhat irregular dilatation surrounded by a condensation of mesoblastic cells. The cloaca is not yet open to the exterior.

On comparing the condition of the organs in this embryo with that in the embryos of *Perameles*, described by Hill,* it will be seen that there is, on the whole, a very close agreement in the stage of development, between the 8.5 mm *Trichosurus* embryo and the 8.75 mm. embryo of *Perameles obesula*.

EMBRYO B (9.5 mm). Plate XXII., fig. 2.

This embryo, which has not as yet been cut, as it is practically in the same stage of development as the following one, is distinctly in advance of Embryo A. The head and fore-quarters are together considerably larger than the rest of the body. The head is much bent on the body. The mouth is widely open and the tongue protruding. The cleft of the mouth extends back to the level of the eye. The nose is well formed and bears a marked resemblance to the nose of the well-developed mammary fetuses, and even to that of the

* J. P. Hill. "The Placentation of *Perameles*," *Quart. Journ. Microsc. Sc.* Vol. xl., p. 385.

adult. No trace of the lachrymal grooves can be detected externally, except, perhaps, the slight notching of the lip. The eyelids give the eye an oval shape, and the slight pigmentation of the retina can be seen. The external ear is already well developed, and a distinct little pointed pinna stands up from the upper and posterior part of the meatus. The anterior limbs are considerably further developed than in Embryo A, and the digits almost meet in front of the chest. Distinct little claws can be detected on the digits. The hind limbs are much in advance of those in Embryo A, and indications of the separate digits can be distinctly made out.

EMBRYO C (10 mm). Plate XXII., fig. 3.

This embryo very closely resembles the preceding. The head is here even more bent on the body. The mouth is almost closed, and the tip of the tongue only but very slightly protruded. The nose and eye are very similar to those in Embryo B, but the ear is apparently a little better developed. The fore limbs are, perhaps, very slightly better developed; but in the hind limbs, though the digits are all marked out, the first and second are less clearly differentiated than in the preceding embryo.

Epidermis.—The epitrichial layer is moderately developed all over the fœtus. It is much less marked on the body proper than on the head and fore limbs. It is especially thick around the snout and anterior part of the lower jaw. The claws may now be regarded as distinctly horny at the tips. The dental lamina is well marked in the front of the jaws.

Skeleton.—The cartilaginous cranium is now fairly well developed. The basi- and exoccipital regions are well chondrified, as is also, to a considerable extent, the periotic capsules. From the basisphenoidal region the trabeculae can be traced forward to the nasal septum with its related nasal cartilages, all of which are already fairly developed. The alisphenoids are separately formed as short rounded cartilaginous bars; and the orbitosphenoids are also already developed. The palate plates, though fairly well formed, are widely apart, and the tongue is found between them,

resting on the base of the nasal septum. Towards the posterior of the palate plates the palato-pterygoid bar can be detected as a narrow semi-cartilaginous rod. Meckel's cartilage is very well developed, and the hyoid arch fairly well, as is also the thyroid. The vertebral centra and arches are more or less chondrified almost to the root of the tail. The ribs are also developed, with the sternum, of which latter, however, the two halves are still considerably apart. The scapula is well chondrified, and the coracoid partly. The clavicle is very distinctly ossified. No chondrification has as yet taken place in the pelvic arch.

Nervous system.—The brain, on the whole, agrees roughly in its degree of development with that of a sheep embryo of 15 mm., though in one or two points the development is more delayed in the marsupial. The hypophysis is quite unconnected with the oral cavity. The spinal cord closely resembles that of Embryo A, though the cellular elements, especially in the anterior half of the cord, are considerably more developed.

Sense organs.—With the exception of its communicating freely with the mouth, the nose agrees essentially with the adult condition. Jacobson's organ is already developed as a tubular epithelial diverticulum. The eye corresponds roughly in its degree of development to that of a human fetus of five weeks (His). The optic stalk has still a fairly wide lumen. The inner wall of the optic cup is fairly thick, and in the outer there is some degree of pigmentation. The lens is relatively considerably smaller than in the corresponding stage of the rabbit or sheep; and has a fairly large cavity. The condition of the internal ear agrees pretty closely with that of the human fetus of five weeks. The cochlea is a moderately long and fairly straight tube. The saccule and utricle are still undifferentiated; while the semi-circular canals are all present as independent canals. The recessus labyrinthi is present as an elongated somewhat club-shaped epithelial process. The taste buds are very distinctly seen on the tongue.

Heart and vessels.—The heart is not developed much in advance of the condition in Embryo A. The septum inferius

does not yet completely divide the ventricles. The septum intermedium, however, is distinctly more developed. The condition of the main blood vessels is very similar: the right and left umbilical veins, though now much closer together, still open independently into the liver.

Lungs.—The degree of bronchial ramification is now considerably in advance of the condition in the seven weeks' human fœtus.

Alimentary canal.—In this embryo the alimentary canal is unfortunately damaged in the region of the umbilicus, but the canal, so far as preserved, differs but little from that in Embryo A. The lumen of the œsophagus, for a considerable distance, is exceedingly small. The pancreas and liver are both fairly well developed.

Urinogenital system.—The mesonephros is considerably further developed than in Embryo A, the tubes being more convoluted, and the glomeruli very considerably larger. The epithelial process representing the pelvis of the true kidney is now markedly lobulated, and well differentiated from the ureter. The genital ridge is much more marked.

EMBRYO D (10·5 mm. as preserved in picro-sulphuric acid).

Plate XXII., fig. 4.

EMBRYO E (11 mm.).

These two embryos are in as nearly as may be the same stage of development. The embryo figured was preserved in picro-sulphuric acid, and measures 10·5 mm., but there is no doubt that, as compared with the other embryos, it has been appreciably more contracted, and that had it been preserved in a similar medium, it would have measured at least 11 mm. Embryo E was considerably damaged on one side, and unfortunately a complete drawing of it was not made before it was cut; but from careful drawings of the head and limbs, the agreement with Embryo D is so marked that it has not been considered necessary at present to cut this latter, which will serve for the description of the external characters; the internal organisation of the same

stage of development being described from the sections of Embryo E.

External characters.—Though the head is flexed on the chest, the neck takes less part in the flexion than in the earlier stages. The cheeks and upper lips are more compressed, and the whole muzzle is more rounded than in Embryos B and C. The lips are fused to a considerable extent, so that the cleft of the mouth instead of being beneath the eye, as in Embryos B and C, is now found beneath a point half-way between the nostril and the eye. The eye is encroached on to a considerable extent by the epitrichial layer, and, though still oval in shape, appears appreciably smaller. The ear resembles the earlier condition, but, like the eye, is becoming encroached upon so that, though the pinna is still quite distinct, the hollow of the external auditory meatus is largely filled by the thickening epithelium. In the figure the fore limb appears almost shorter than in Embryo C, but this appearance is partly due to the skeletal elements meeting in front, and partly to the increased epithelial growth, as the digits could now quite easily interlock. The claws are well marked. The hind limbs are not yet much more advanced than in Embryo C, but the digits are rather more distinctly mapped out.

Epidermis.—Besides the increase of the epitrichial layer, the most noteworthy additional feature met with in this stage is the presence of well marked hair anlagen on the sides of the snout. These are present as proliferations and dippings down of the cells of the Malpighian layer, with condensations of the subjacent mesoblastic cells. The dental lamina extends round a considerable distance on both jaws, and the dental germs of the first upper incisors are well differentiated.

Skeleton.—Except in the more complete chondrification of the various elements the skeleton differs but little from that of Embryo C. The coracoid is now chondrified to its inner end. In the lower extremity the femur and pelvic elements, though not yet cartilaginous, can be distinctly traced. Ossification is just commencing in the maxillary bone.

Nervous system.—The brain and spinal cord do not differ greatly from those in Embryo C. The central canal of the cord is still of great size, and occupies $\frac{7}{9}$ of the antero-posterior diameter of the cord. It is considerably dilated at its posterior end, so that the canal on section is club-shaped. Cellular elements (presumably spongioblasts) are very abundant round the posterior part of the canal. The anterior cornu of grey matter is very much larger than the posterior.

Sense organs.—The nasal cavity is now well developed, though still communicating freely with the mouth. Jacobson's organ is likewise well formed and rests on the now chondrified parasепtal cartilage. The eye has not advanced much from the condition in embryo C. There is still a fairly wide lumen in the optic stalk, but the lumen of the lens is appreciably smaller. In the ear the saccule and utricle are now to some extent differentiated from one another. The semicircular canals are well formed.

Heart and vessels.—The division of the ventricle is not yet quite complete, but the aortic bulb is considerably further subdivided than in Embryo C. The chief blood vessels, with the exception of those belonging to the distinctively foetal circulation, agree in the main closely with the adult condition. The right umbilical vein is still present, but it no longer opens into the liver, and merely serves to convey some of the blood from the anterior abdominal wall to the sinus along the posterior border of the umbilicus.

Lungs.—The bronchi are now well subdivided, and the lungs are of fair size. The two main bronchi have the mucous membrane arranged in longitudinal folds.

Alimentary canal.—The œsophagus has a distinct lumen throughout its whole extent. The stomach, duodenum, and upper part of the small intestine are well developed, and in this part of the intestine the mucous membrane is very much folded. In the lower half of the small intestine the lumen is comparatively small, and the mucous membrane is free from folds. There is still a trace of the vitelline duct, and in the neighbourhood of the duct the intestine is slightly more dilated. The cæcum, though

relatively longer than in Embryo C, is considerably narrower, as is also the upper part of the great intestine generally. The rectum is now distinctly open.

Urinogenital system.—The mesonephros is relatively very large, and the tubules very much convoluted. The Muellertian ducts are laid down for a very short distance. The germinal epithelium is well developed, but sexual differentiation is not apparent. The condition of the permanent kidney is very similar to that in Embryo C; the sprouting is, however, somewhat more marked.

EMBRYO F (14 mm). Plate XXIII, fig. 5.

This embryo has already been figured by Dr. Beard in the paper above referred to, but as his illustration is not very carefully done, and contains a number of inaccuracies, I have thought it well to refigure the embryo. This and the following embryo well illustrate the degree of development just before birth. The epitrichial layer is so far developed that the eye and ear are almost completely obscured: the position of the eye, however, can be distinctly made out owing to the pigmentation still being visible through the epithelial layer. In Dr. Beard's illustration a certain obscure shading is evidently intended to represent the position of the eye, but the eye is considerably nearer the nostril than is indicated in the drawing. The lips are almost united laterally to form the "Saugmund," but not yet completely. The head is still folded slightly on the chest. The arms and hands are in much the same position as in the earlier embryos—folded across the chest. The claws are now well developed. The hind limbs are still small, though the digits are very distinctly formed and partly separated from each other. The hallux stands prominently out and about equals in size the 2nd and 3rd digits, while the 4th and 5th digits are each about one-half larger than the others. In Dr. Beard's figure the 2nd and 3rd digits are shown as fairly large, and the 4th and 5th quite rudimentary.

Epidermis.—The epitrichial layer is fairly well developed over the whole body, but is especially marked on the snout, sides of head, and fore-limbs. Hair follicles are present in those situa-

tions where enlarged hairs (? tactile hairs) are met with in the later mammary fœtuses. The dental lamina can be traced back to the plane of the eye, and the dental germs of the anterior teeth are well differentiated.

Skeleton.—The cartilaginous skeleton is almost completely formed. The pelvis and the skeleton of the posterior extremities are fairly well chondrified, and the vertebral centra can be traced for a considerable distance along the tail. The sternum is developed, but at its lower half the two sides are not yet completely united. The coracoid is well developed and articulates with the sternum, and the clavicle is well ossified. The chondrocranium is complete, and the following bones are well ossified—premaxillaries, maxillaries, palatines, and mandibles.

Nervous system.—The brain and spinal cord are not very satisfactorily preserved in this embryo. In the cord the grey columns are still further developed, giving the cord on section a more rounded appearance. The central canal still extends to the posterior part, and there is as yet no trace of a posterior fissure.

Sense organs.—The nose is well formed, and as the palate is now closed, the appearance differs but little from that of the adult, save that the turbinals are as yet rudimentary. The eye is still but imperfectly developed. The retina is a fairly thick layer, and is not yet differentiated in its structure. The pigmented layer is only pigmented in its anterior two-thirds. The optic stalk still has a distinct lumen. The internal ear is fairly well developed—the saccule and utricle are quite distinct, the semicircular canals well formed, and the cochlea of large size, though still but slightly curved.

Heart and vessels.—The two ventricles are now completely divided, and the aortic bulb is likewise completely subdivided. The pulmonary arteries arise from the pulmonary in a common though exceedingly short stem. The apparent difference in the mode of origin of the arteries from that in the earlier embryos is due to the points of origin becoming approximated with the lengthening of the embryo and their ultimately coinciding. The left umbilical vein now lies almost in the middle line, and the

right vein is practically lost, though it can still be detected as an exceedingly minute vessel.

Lungs.—In the earlier embryos the bronchial tubes appear as moderately simple tubular processes, but at this stage the terminal tubules have become enlarged into irregular saccular dilatations, along the borders of which further budding is taking place into the mesoblastic tissue.

Alimentary canal.—The oesophagus is very well formed, and has a moderately wide lumen throughout its whole extent. The rest of the canal resembles closely that in Embryo E. The stomach and upper part of the small intestine are better developed, and the caecum is larger and more dilated.

Urinogenital system.—The mesonephros is not much larger than in Embryo E, nor are the tubules more convoluted. The Muellerian ducts are, however, considerably further developed, and the permanent kidney is much advanced, the uriniferous tubules becoming distinctly developed. The genital gland is fairly large, but it has apparently not yet become sexually differentiated.

EMBRYO G (14 mm). Plate XXIII., fig. 6.

This beautifully preserved embryo, though of similar size to the preceding, and quite ready to be born, differs in one or two points. The head is lifted up from the chest and is in a similar attitude to that in the newly born embryo. Though this specimen was removed from the uterus and has the membranes still attached, it has in all probability breathed, and the tip of the tongue is hollowed, as if endeavours had been made to grasp the expected nipple. The fore limbs no longer cross in front of the chest, but hang down as if ready to catch on to the mamma. The hind limbs come well forward and are well developed, the different digits being well shown. The body is considerably larger than in Embryo F, which I think due to this embryo's having breathed. There is one interesting point about this specimen, in that the epitrichial layer has not quite completely

covered the eye—a minute slip being still left between the eyelids.

EMBRYO H (14·8 mm). Plate XXIII., fig. 7.

This embryo is a very good example of the newly born condition. I have in my possession six embryos in which part of the umbilical cord is still attached, and all of which may be regarded as newly born. Of these the greatest lengths are 13 mm., 13·8 mm., 14·5 mm., 14·8 mm., 15·2 mm., and 15·4 mm. As these embryos have all been similarly preserved, it will be seen that there is some slight variation in the exact size at birth, but that the average size is a little over 14 mm. Even at this very early stage when the little embryo is removed from the teat it makes clawing movements with its fore limbs as if endeavouring to pull itself on to the teat again; and as a result of this the fore limbs in the preserved specimens are found in very various attitudes. The palms are usually turned more or less downwards and inwards, and the limbs project forwards. In one specimen, however, the limbs are raised, and the back of the right hand almost touches the side of the head. The claws are very sharp and fairly long. In most specimens the head is well raised—its axis being at right angles to that of the body. The epitrichial layer is so thick that the eye can only with difficulty be made out, while the ear is completely covered over and only indicated by the folded pinna causing a little projection. The posterior portion of the embryo is usually curved forwards so that the hind limbs are made to point forwards and somewhat upwards. The digits of the posterior limb are all well marked out and partly separated—the 4th and 5th digits being distinctly the larger. The tail is comparatively short. Between the two posterior limbs is found a projection which looks like a well marked penis. But not only at this stage, but for long after, not the slightest difference can be seen, at least externally, between the penis of the male and the clitoris of the female. (Note the well marked clitoris in the female embryos shown in figs. 11 and 12). There is as yet no trace of the pouch or scrotum externally.

Epidermis.—The epitrichial layer is moderately thick all over the body; but, as in the previous embryo, the layer is thickest on the head and fore limbs. The hair follicles of the large hairs of the head and fore limbs are well formed, but there is no trace as yet of the follicles of the body hairs. The claws of the digits of the anterior limbs are well formed, but on the posterior digits, though the epithelium is thickened at the tips, there is no distinct evidence of claws. The anterior dental germs are well formed, and the dental lamina can be traced well back.

Skeleton.—The cartilaginous skeleton is almost complete. The vertebral centra are chondrified well into the tail, and in the upper vertebral region the notochord is almost obliterated except in the inter-vertebral discs. The neural arches do not yet meet, however. The upper limb is completely formed, and the coracoid well chondrified to its attachment with the sternum. The lower limb is almost completely formed, the phalanges and the tarsal elements being chondrified. The chondrocranium may be regarded as complete, and the following bones are well ossified—premaxillaries, maxillaries, palatines, pterygoids and mandibles.

Nervous system.—The brain is taking on the adult characters. The choroid folds into the lateral ventricle, is partly formed, and the paraphysis well marked. Though the corpus striatum and optic thalamus can be detected, they are not as yet well formed. The spinal cord on section is almost round. The central canal is still very large, and on section somewhat club-shaped. The cellular elements are much more numerous round the posterior half than on anterior; the anterior grey columns are, however, larger than the posterior, so that the whole grey matter of the cord becomes on section almost round. The anterior and posterior white columns are both fairly well formed, but contribute still further to giving the cord a rounded appearance. There is as yet no trace of a posterior fissure.

Sense organs.—The nose is well formed, though the turbinals are as yet but imperfectly formed. Jacobson's organ is well formed, and is typically marsupial in character. The eye is still imperfectly formed. The layers of the retina are not yet

differentiated; in the anterior two-thirds only of the pigment layer is pigmentation present; there is still a lumen in the lens; and a very minute lumen can still be traced in the optic stalk. The internal ear much resembles that in the previous embryo, but here, though the cochlea is still moderately straight at its anterior end, the first indications of coiling have commenced.

Heart and vessels.—At birth the permanent circulation becomes established, and even already in this specimen the ductus arteriosus is no longer patent, and the umbilical vein is obliterated. The foramen ovale is closed.

Lungs.—The lungs at birth exhibit a very interesting condition. The bronchi are as yet but very imperfectly formed, and the ramifications but few, and as the lungs have at this early stage of development to be functional, the bronchi have become dilated into very large irregular air-spaces to increase the surface of the mucous membrane. The trachea and the upper part of the two main bronchi are supported by imperfect cartilaginous rings. The air-sacs open either directly into the main bronchi or into the secondary bronchi. Connected with the bronchi are numerous comparatively small irregular tubular ramifications, which probably represent the further development of the bronchial system, and which as yet are probably not functional.

Alimentary canal.—The alimentary canal is now well formed, and in the stomach and small intestine are coagula of milk. The small intestine is of large size to near its lower end. It is arranged in about four very irregular coils. Its lower 6th is comparatively small. The cæcum is still small, though considerably longer than in the earlier embryos. The colon is relatively small and simple. Judging from the structure of the alimentary canal it seems probable that all the milk ingested becomes absorbed before reaching the colon, and that the cæcum and colon are not functional till a much later period.

Urinogenital system.—The mesonephros is still of very large size, and the tubules very much convoluted. At this stage, and probably for some time afterwards, the entire excretory function

is performed by the Wolffian bodies. The true kidney is developed much in advance of the condition in Embryo F, though still much too imperfect to be functional. The upper end of the kidney is almost on a level with the top of the Wolffian body, and on the right side is practically in contact with the liver. The Muellerian duct can be traced for nearly half a millimètre. The suprarenal bodies are of large size. The genital glands are of considerable size, and the sex may possibly be differentiated, but I should like to examine more than one embryo of this stage, and some later specimens in which the sex is undoubtedly defined before being sure on this point.

In describing this and the earlier embryos there are one or two points which I have refrained from dealing with, such as the mammary glands, thymus, thyroid, &c., as a further examination will require to be made of later stages before the early condition of the mammary glands can be satisfactorily understood; and though the earliest embryos here described show the thymus and thyroid in very interesting conditions, still earlier specimens will be required to show their modes of development.

Later Mammary Fœtuses.

With the limited time at my disposal it is practically impossible for me at present to follow the later development of the various organs throughout the developing mammary fœtuses; but as opportunity offers the developmental history of certain structures will be fully traced. At present I am engaged in working out the development of the shoulder girdle and of the skull, and trust shortly to be in a position to give an account of the development of the mammary glands and pouch. As many of the post-natal stages will be used in future work, and as there is much of interest in the external anatomy, I have thought it well to give a description of a number of typical examples of the smaller mammary fœtuses.

The most noticeable change that takes place in the embryo shortly after birth is a considerable increase in size of the abdominal region. This is doubtless due to the greater development

of the small intestine, and to the distention of the stomach and intestines with the ingested milk. This feature is well shown in the embryo of 16 mm., greatest length, shown in Plate xxiii., fig. 8. This embryo, though but little longer than the newly-born specimen, is, owing mainly to the abdominal distention, of much greater bulk. The epitrichial layer is apparently rather thicker, so that the position of the eye can scarcely with certainty be made out. The umbilicus is quite healed, but the scar is still distinct. There is as yet no indication of the pouch or scrotum. The following are some of the principal measurements:—Head length, 7 mm.; snout to root of tail, round the dorsal curve, 28.5 mm.; tail, 4.5 mm.; arm from elbow to tip of middle digit, 5.7 mm.; leg from knee to tip of 4th digit, about 3.5 mm.; foot, about 2 mm.

Beyond a general increase in size there is little change in the external appearance of the mammary fetus for some time. A fetus of 19 mm., greatest length, is shown in Plate xxiv., fig. 9. The two chief points of interest in this embryo are that rudimentary claws are now distinctly present on the four toes of the hind foot, and that, whereas at birth and for a short time afterwards, the nipple is grasped by the tongue and upper lip, here and in all the later stages, the tongue is entirely within the mouth, and the nipple is grasped between the upper and lower lips. The umbilical scar is still apparent, but as yet there is no evidence externally of the sex. The principal measurements of this embryo are:—Head, 7.5 mm.; snout to root of tail, round the dorsal curve, 32 mm.; tail, 5.5 mm.; arm, 6.5 mm.; leg, 4.3 mm.; foot, 2.5 mm.

Shortly after this stage important changes begin to be manifested in the external characters. With the relatively rapid growth of the hind limb flexion takes place at the knee and ankle, clearly differentiating the parts of the limb. But a more important character is the manifestation of sex by the development of the scrotum in the male, and of the pouch in the female. In both male and female embryos the sexual characters become manifested about the same time, viz., when the embryo attains to 23 mm. in greatest length. Doubtless, microscopic examination

will reveal the different characters at a considerably earlier stage, but while in an embryo of 20 mm. or even 22 mm. it is impossible to tell the sex from external examination, in an embryo of 23 mm. this can usually be told, and there is not the slightest difficulty in any of the later stages.

A beautifully preserved male embryo of 23·8 mm., greatest length, is shown in Plate xxiv., fig. 10. In most respects this embryo resembles the earlier stage figured, but the distinct advance can be seen in the further development of the hind limbs. The umbilical scar can still be made out, but is well covered with epithelium. In the lower part of the abdomen and extending across the middle line is a somewhat indistinct bilobed slight elevation. This is the earliest external manifestation of the scrotum. The following are the principal measurements at this stage:—Head, 9·5 mm.; snout to tail, 38 mm.; tail, 6 mm.; arm, 8 mm.; leg, 5 mm.; foot, 3·5 mm.

In the female embryo the pouch begins to appear as a median depression in the lower part of the abdominal region.

Plate xxiv., fig. 11, represents a female embryo of 27 mm., greatest length, with the nipple still retained in the mouth. The pouch is well marked, and the clitoris is large and still indistinguishable externally from the penis in the male. The pinna of the ear is beginning to free itself from the epitrichial layer. In addition to the claws on four toes of the hind foot, a rudimentary claw can now be detected on the hallux. There are as yet no external indications of hair. The following are the principal measurements:—Head, 10 mm.; snout to tail, 41·5 mm.; tail, 7 mm.; arm, 10 mm.; leg, 6 mm.; foot, 3·8 mm.

In an embryo of 30 mm., greatest length, hair has already appeared on the sides of the head, along the shoulders, down the arms as far as the elbows, and along the sides of the body to the lower part of the chest. The pinna of the ear, though still closely applied to the side of the head, is practically free. The principal measurements at this stage are:—Head, 12 mm.; snout to tail, 47 mm.; tail, 8·5 mm.; arm, 11·5 mm.; leg, 7·5 mm.; foot, 4 mm.

In an embryo of 36 mm., greatest length, or from head to rump, 33.5 mm., hair is found over most of the body, with the exception of the following regions, which are hairy later, and which are still bald,—a median strip from the forehead to between the shoulders, sides of the mouth, ears, backs of the hands, margins of the pouch, hind legs except on outer surfaces of knees where hair is just appearing, tail and perineal region. The vibrissæ are now seen, but none of the other large hairs. Though hairs are thus present over the greater part of the surface, the embryo not only at this stage, but for long after, on superficial examination looks quite naked. This is owing to the hairs being very fine and short, and also very few in number. When the surface is examined by the low power of the microscope the minute hairs are seen to be regularly arranged, and each from one-half to one-third of millimètre distant from its neighbour. The principal measurements at this stage are:—Head, 14 mm.; snout to tail, 57 mm.; tail, 12 mm.; arm, 13 mm.; leg, 9.5 mm.; foot, 5 mm.

In embryos larger than the preceding, the greatest length gives but a very imperfect idea of the size, as owing to the length and flexibility of the body the embryos are found variously curved. The embryo shown in figure 12 measures in a direct line from head to rump, 40 mm., or to the curve of the tail, 43 mm. As showing the irregularity in development, the vibrissæ in this embryo are not yet through the surface, although the embryo is very distinctly larger than the preceding. The body hairs are very similarly developed; the bald patch on the back of the head is smaller in size. There is still no hair on the backs of the hands, on the feet, tail, or ears. The claws on the hind toes are very well marked, and the little claw or nail on the hallux quite distinct. The pinna of the ear is now quite free and folded forwards. The line of the united eyelids can be distinctly made out. The following are the principal measurements:—Head, 15 mm.; snout to tail, 62 mm.; tail, 15 mm.; arm, 15 mm.; leg, 12 mm.; foot, 6 mm. The rapid proportional growth of the hind quarters

will be noticed, as exemplified by the measurements of the leg, foot, and tail.

The two embryos shown in Plate xxv., illustrate the later development of the mammary fœtuses. The most striking feature here shown is the rapid growth of the hind limbs and tail. Another point that will be noticed is the change of attitude of the pinna of the ear. In all the early embryos it is directed forwards, but shortly after it becomes free from the epitrichial layer it increases greatly in size, and becoming somewhat more flexible it, as a rule, becomes folded backwards. Though this is the case in the large majority of embryos, occasionally the ears continue to be directed forwards till a late stage in development. In the large embryo shown in fig. 14 the right ear is folded back, while the left is still directed forwards.

In the smaller of the two late mammary fœtuses shown in fig. 13, hair is to be found practically all over the body. The hair, however, is scarcely longer, nor are the hairs more closely together than in the earlier embryos, so that the body still looks, at first sight, quite naked. The vibrissæ are of large size, and the enlarged hairs above and below the orbits are also well developed. The wrist enlarged hairs and those under the lower jaw are also showing, but the ankle hairs are not yet through the surface. The claws on the two outer toes of the hind feet are of large size, those of the syndactylous toes small but well formed, while the little claw of the hallux, instead of being more developed, is rather less marked than in some of the earlier stages. The following are the principal measurements at this stage:—Head, 23·5 mm.; snout to tail, 99 mm.; tail, 30·5 mm.; arm, 24·5 mm.; leg, 23·5 mm.; foot, 10·5 mm.

The embryo shown in fig. 14, with the exception of its being still scantily clad with hairs differs but little in its character from the adult. The eyelids, though still closed, may be said to be fully formed, and the lips, though they are still closely cemented except in front, as indeed they are till a much later period, can be pulled apart without apparent injury. This embryo is a female. There is a deep pouch, and the clitoris is still

large and external. Though hair is found on all the parts where hair is found in the adult, the hairs are so small that the embryo still looks quite naked. With the exception of the vibrissæ, the few large specialised hairs in other parts, and some longer hairs round the lips, none of the body hairs is longer than half a millimètre, and almost all the hairs are situated at least half a millimètre apart. The vibrissæ are well developed, and large specialised hairs are also found in the following situations:—Two large hairs above each eye, a row of five large hairs on the cheek under and a little behind each eye, a couple from a median papilla on the posterior part of the symphysis of the lower jaw, a couple from a papilla on the extensor surface of the forearm near its middle, a bunch of 8 or 9 from a large papilla near the union of the middle with the lower third of the flexor surface of the forearm, and a couple of large hairs which spring from the inner side of each heel. All these enlarged hairs are at least 6 mm. in length, and the vibrissæ are mostly a trifle over 10 mm. in length. The claws of the syndactylous toes are not yet specialised, though large and well formed. The following are the principal measurements at this stage:—Head, 34 mm.; snout to tail, 127 mm.; tail, 57 mm.; arm, 36 mm.; leg, 34 mm.; foot, 17 mm.

REFERENCES TO FIGURES.

Plate XXII.

Trichosurus vulpecula.

- Fig. 1.—Intra-uterine fœtus, 8.5 mm., g.l. (damaged). Embryo A.
 Fig. 2. ,, ,, 9.5 .. ,, Embryo B.
 Fig. 3. ,, ,, 10 .. ,, ,, C.
 Fig. 4 ,, ,, 10.5 .. ,, ,, D.

Plate XXIII.

- Fig. 5.—Intra-uterine fœtus. 14 mm., g.l. Embryo F.
 Fig. 6. ,, ,, 14 .. ,, ,, G.
 Fig. 7.—Newly born mammary fœtus, 14.8 mm., g.l. Embryo H.
 Fig. 8—Mammary fœtus, 16 mm., g.l.

Plate xxiv.

- Fig. 9.—Mammary fœtus, 19 mm., g.l.
 Fig. 10. " " 23·8 mm., g.l.
 Fig. 11. " " 27 mm., g.l., (with nipple).
 Fig. 12. " " 15 mm., head length, (with nipple).

Plate xxv.

- Fig. 13.—Mammary fœtus, 23·5 mm., head length.
 Fig. 14. " " 34 mm. "

Figs. 1-13 variously magnified; fig. 14 natural size.

— Figs. 1, 2, 3, 4, 6, 9, 10, 11, 12, 13 and 14 are drawn from nature; figs. 5, 7 and 8, from photographs by Dr. Beard.